

A NEW POLYSEPTATE THECIDEACEAN BRACHIOPOD FROM THE MIDDLE JURASSIC OF THE COTSWOLDS, ENGLAND

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ABSTRACT. Study of material from a new locality reveals the presence of an Aalenian thecideacean which, in its morphology and shell microstructure, is similar to certain upper Jurassic and lower Cretaceous species. The new Aalenian specimens are assigned to *Mimikonstantia sculpta* gen. et sp. nov. because of the doubtful validity of the upper Jurassic genus *Konstantia* Pajaud 1970. Although impunctate, the shell microstructure, with its suppressed secondary fibrous mosaic, closely resembles that of the lower Cretaceous *Thecidiopsis tetragona* (Roemer) and *T. lata* Smirnova. It is therefore considered that *Mimikonstantia*, *Konstantia*, and *Thecidiopsis* are phylogenetically linked. The evidence obtained from the study of *M. sculpta* enables the onset of the neotenus suppression of the secondary fibrous shell layer to be placed much earlier in the history of the Thecideidina than has previously been suspected.

DURING investigation of the shell microstructure of thecideidine brachiopods of Aalenian age from a number of localities in the Cotswolds, collections were obtained from Salterley Grange Quarry (grid ref. SO 946 177) and Crickley Hill (grid ref. SO 928 163) near Cheltenham, in which the majority of the specimens could be assigned to previously described species of *Moorellina* Elliott 1953. However, a small number of brachial valves were noticed which showed a septal arrangement previously unrecognized in lower Inferior Oolite species. Lack of material, however, prevented their systematic study until collections were subsequently obtained from a locality in a small overgrown quarry (grid ref. SO 832 036) on Selsley Common near Stroud.

At the localities mentioned, specimens were collected from the upper part of the Pea Grit (upper Aalenian), lithologically a medium to coarse grained shelly pisolite (pisomicrite of Morris 1980) with occasional coralliferous horizons and hardgrounds overlain by more loosely consolidated marly horizons. It was from these marly horizons that the collections were obtained. Thecideidines were found to be a particularly common element of the Selsley fauna and a collection of 1,332 brachial valves was obtained of which 15% (200) belonged to a form resembling the upper Jurassic genus, *Konstantia* Pajaud 1970. A detailed study of the specimens revealed the presence of a new genus, necessarily described by reference mainly to the characters of separated brachial valves, due to the usual problems involved in the accurate identification of complete thecideidine shells and pedicle valves (Baker and Laurie 1978, p. 557).

Registration of material. The holotype, paratypes, and topotypes, together with sectioned material are housed in the British Museum (Natural History) under numbers BB 84690–BB 84701

Preparation of material. Bulk samples of pisolitic marl were initially washed to remove clay-grade sediment. The residue was dried and passed through a nest of 2.4 mm, 1.68 mm, 850 μm , 500 μm , and 350 μm sieves. The thecideidines were then hand-picked from the sieved residues under a binocular microscope. The majority of specimens were obtained from the 850 μm and 500 μm sizes. The *Konstantia*-like specimens were then carefully cleaned under water, using tweezers, a surgical needle, and a very fine brush. Owing to the risk of damaging the thin and often already cracked shells sonication was not attempted. Specimens selected for sectioning were gold-coated, photographed using a scanning electron microscope for the purpose of obtaining a photographic record, and mounted in cold setting resin. Figured material was also gold-coated prior to photomicrography. The characters depicted in text-figs. 1–3 were traced from actual specimens with the aid of a 'Wild' stereomicroscope fitted with a drawing tube.

SYSTEMATIC PALAEOLOGY

Order UNCERTAIN

Suborder THECIDEIDINA Elliott, 1958

Superfamily THECIDEACEA (Gray, 1840) H. and G. Termier, 1949

Family THECIDEIDAE Gray, 1840

Subfamily THECIDEINAE (Gray, 1840) Dall, 1870

Genus MIMIKONSTANTIA gen. nov.

Diagnosis. Impunctate, polyseptate thecideinin having brachial cavities devoid of brachial lobes and the pedicle valve with a characteristic marginal rim with tuberculate inner and smooth outer zones.

Description. Small, wider than long, ventribiconvex, the pedicle valve with a relatively large attachment scar and well-developed free ventral wall; ventral interarea relatively small, pseudodeltidium ill-defined; anterior commissure straight; growth lines obscure; impunctate. Pedicle valve interior with strong teeth and dental ridges united with raised hemispondylium; marginal rim with tuberculate inner and smooth outer zones. Brachial valve interior with small, weakly bilobate cardinal process; bridge abutments sharply angled but with no positive evidence of a brachial bridge; brachial cavities without brachial lobes, the brachial apparatus consisting of four or five approximately radially disposed septa in contact with the anterior and antero-lateral border of the valve.

Age. Middle Jurassic, Aalenian

Etymology. From the Greek *mimikos* (mimic) after the development of the polyseptate anterior without any trace of brachial lobes in the brachial cavities.

Type species. *Mimikonstantia sculpta* sp. nov.

Mimikonstantia sculpta sp. nov.

Plates 69, 70, and 71; text-figs. 1–4, 5A

Diagnosis. *Mimikonstantia* up to about 2.5 mm in length, 3.5 mm in width, and 1.5 mm in thickness. Outline transversely elliptical, typically with the width approaching one and a half times the length. Anterior commissure straight, or with a very slight invagination.

Dimensions of holotype. Length 1.8 mm, width 2.6 mm, thickness 0.5 mm.

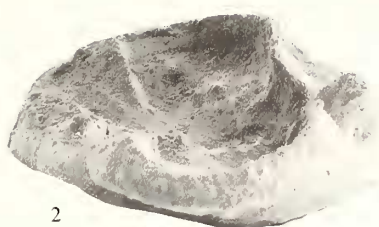
Distribution. Geographic distribution unknown but probably local in its occurrence. Stratigraphically the species occurs near the top of the Pea Grit (Aalenian, *murchisonae* Zone, *murchisonae* Subzone) at Salterley Grange Quarry (grid ref. SO 946 177), and Crickley Hill (grid ref. SO 928 163) near Cheltenham, also at Selsley Common (grid ref. SO 832 036) near Stroud.

EXPLANATION OF PLATE 69

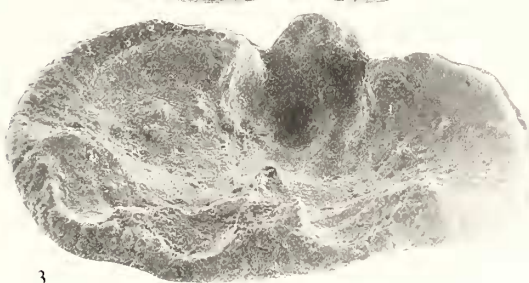
Figs. 1–8. Stereoscan photomicrographs of specimens of *Mimikonstantia sculpta* gen. et sp. nov. from the Pea Grit, Selsley Hill, near Stroud. All figures are of specimens coated with evaporated gold before photography. 1–3, brachial, lateral, and anterior views of the holotype BB 84690, $\times 25$. 4, enlarged portion of the margin of pedicle valve BB 84693, showing the ornamented internal surface of the free ventral wall and the tuberculate inner and smooth outer zones of the marginal rim; ornament and tubercles slightly abraded in this specimen, $\times 160$. 5, interior view showing the morphology of the pedicle valve of paratype BB 84693, $\times 25$. 6, brachial view of a matrix-filled brachial valve, paratype BB 84691, showing the blade-like extensions of the septa. The left (as viewed) lateral septum (arrowed) has been fractured and compressed sideways during diagenesis of the sediment, $\times 30$. 7, brachial view of a complete specimen, paratype BB 84694, showing the relationship between the fragile flange round the brachial border, left antero-lateral sector, and the way in which breakage results in the exposure of the characteristic marginal rim, right antero-lateral sector, of the pedicle valve, $\times 25$. 8, brachial view of a bryozoan-encrusted brachial valve, paratype BB 84692, showing a mould of the complete brachial flange. The apparent pores are really rhomb-shaped diagenetic structures (see Pl. 71, fig. 1), $\times 20$.



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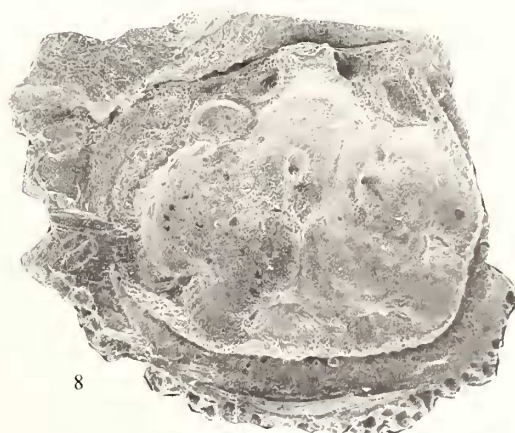
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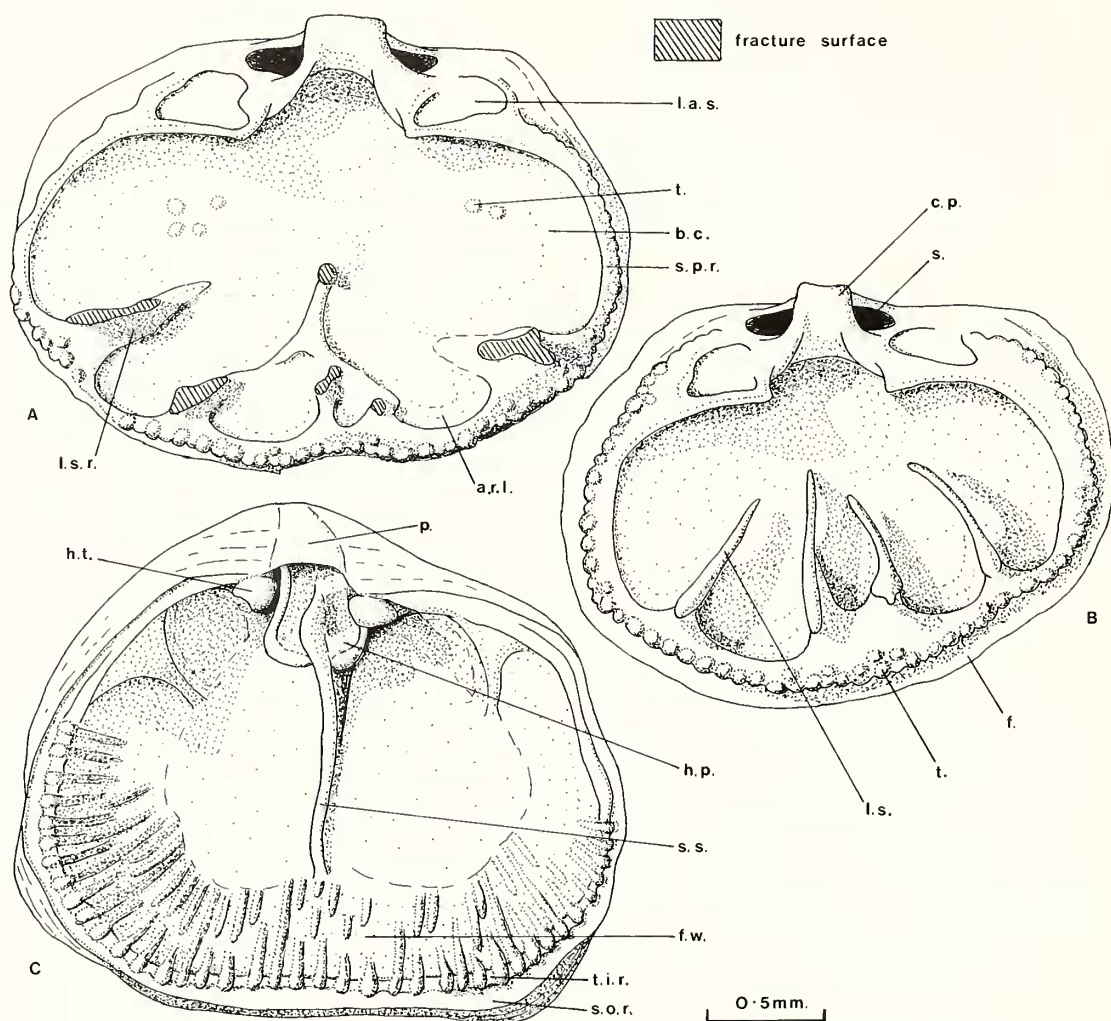
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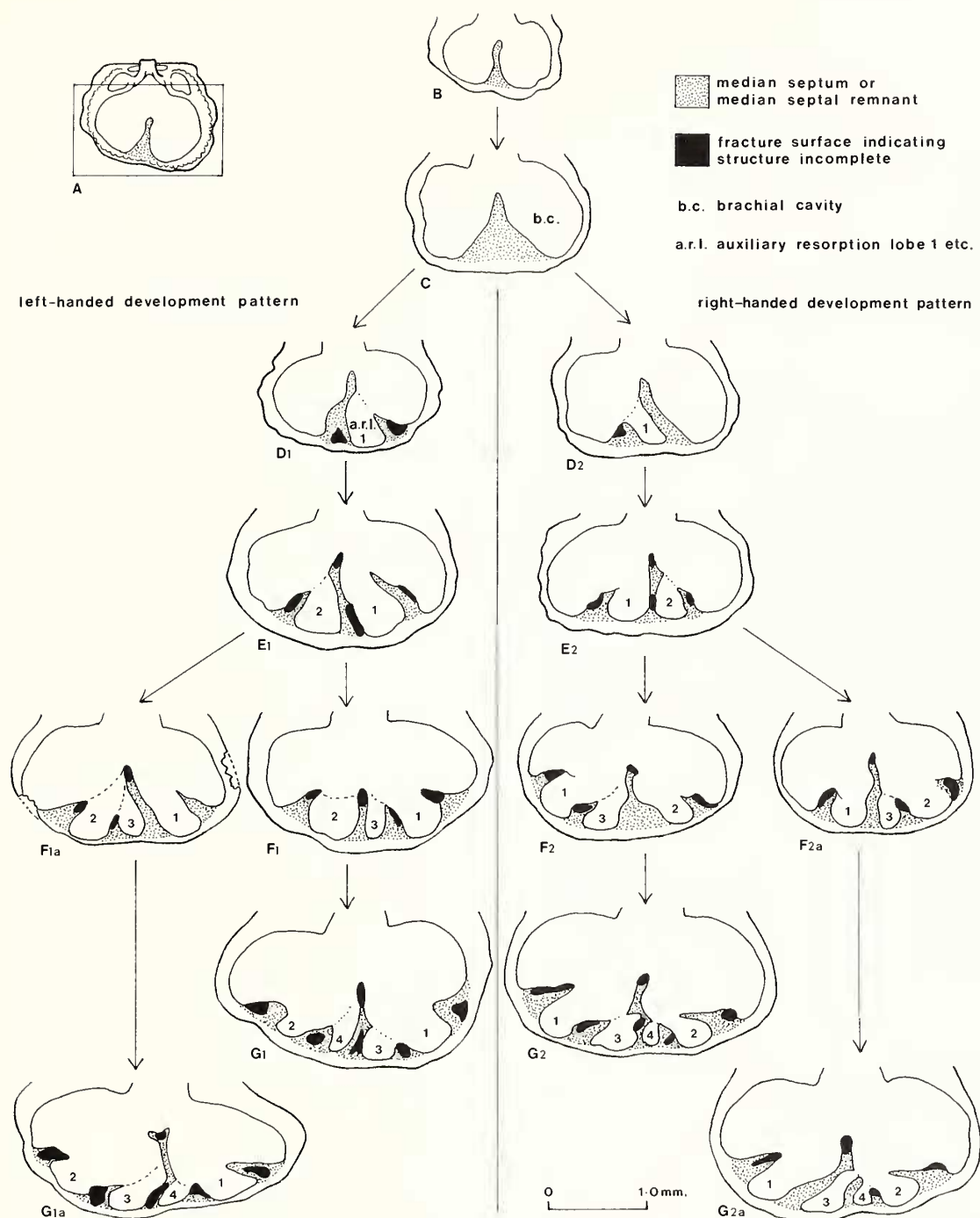
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TEXT-FIG. 1A, 'Wild' stereomicroscope trace of the holotype of *Mimikonstantia sculpta* gen. et sp. nov. (BB 84690) to show the lateral septal remnants, typical of the adult brachial valve in its separated state. B, reconstruction of the adult brachial valve based on specimens BB 84690–BB 84692 and sectioned specimen BB 84698 to show the form of the lateral septa and the delicate peripheral flange. C, reconstruction to show the typical internal morphology of the pedicle valve, based on a stereomicroscope trace of paratype BB 84693. Tuberculate rim enhancement incorporated from specimen BB 84694. a.r.l. = auxiliary resorption lobe, b.c. = brachial cavity, c.p. = cardinal process, f. = flange, f.w. = free ventral wall, h.p. = hemispondylial plate, h.t. = hinge tooth, l.a.s. = lateral adductor muscle scar, l.s. = lateral septum, l.s.r. = lateral septal remnant, p. = pseudodeltidium, s. = dental socket, s.o.r. = smooth outer rim, s.p.r. = sub-peripheral rim, s.s. = hemispondylium supporting septum, t. = tubercle, t.i.r. = tuberculate inner rim.



TEXT-FIG. 2. Series of drawings to show the development of the brachial supports in *Mimikonstantia sculpta*. A, locational diagram. B, C, early juveniles showing the development of the initial median septum. D, juveniles showing the thickened median septum invaded by an auxiliary resorption lobe (a.r.l. 1) extending from the left, D₁ and right, D₂, brachial cavities. E-G, left- and right-handed sequences showing the repeated division of the median septal remnant by progressive invasion by a succession (a.r.l. 2-4) of auxiliary resorption lobes as growth proceeds. Left-handed and right-handed defined anatomically, not as viewed.

Derivation of name. From the sculpturing of the polyseptate anterior of the brachial valve through the repeated invasion of an initially thickened median septum by a succession of resorption fronts.

Type specimens. Holotype BB 84690 and paratypes BB 84691–BB 84694

Description. A small ventribiconvex thecideinin with a moderately large attachment scar and well-developed free ventral wall giving rise to a depressed triangular lateral profile. The ventral interarea is reduced and indistinct with an ill-defined flat to slightly convex pseudodeltidium. There is no trace of an interarea in the brachial valve and the growth lines are usually indistinct.

MORPHOLOGY, GROWTH AND SHELL MICROSTRUCTURE

Characters of pedicle valve

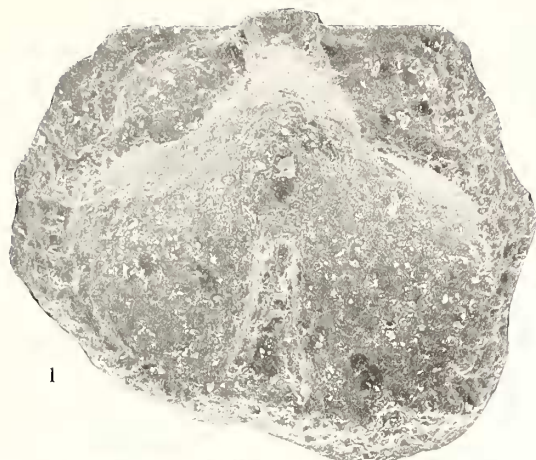
A raised hemispondylium is normally present with clearly defined dental ridges, hemispondylial plate, and a supporting septum (Pl. 69, fig. 5; text-fig. 1c) which extends anteriorly almost to the base of the free ventral wall. The teeth are typically thecideidine (Jaanusson 1971) and not widely separated. The internal surface of the free ventral wall is ornamented with ridges and grooves. The ridges, which are often slightly beaded, terminate near the commissure in a zone of tubercles which forms the inner part of a double marginal rim (Pl. 69, fig. 4). The outer part of the rim consists of a smooth flange which corresponds with a similar flange developed round the border of the brachial valve (text-fig. 1b). The floor of the valve, corresponding approximately with the area of attachment externally, is smooth with well-defined lateral adductor muscle scars on each side of the hemispondylium. The shell substance is impunctate.

Characters of brachial valve (Pl. 69, figs. 1–3; text-fig. 1A, B).

The brachial valve is transversely elliptical with a maximum width in the order of 3.5 mm. The posterior cardinal border is approximately two-thirds of the valve width. The cardinal process is small, weakly bilobate, and bounded by typically thecideidine dental sockets with its dorsal surface aligned almost perpendicular to the plane of the commissure (Pl. 70, figs. 2, 4). The lateral adductor muscle scars are oval and quite deeply impressed. The bridge abutments are quite sharply angled on well-preserved valves but no positive evidence of a bridge has been found, even in sectioned complete shells. The brachial cavities are shallow and, in the sense that the brachial supports do not arise from their floor, are without brachial lobes. The brachial apparatus consists of a maximum of five approximately radially disposed septa which are almost invariably broken in separated valves. Sectioned complete shells and occasional matrix-filled brachial valves (Pl. 69, fig. 6; text-fig. 1b), however, show that the majority of the septa, continuous with the sub-peripheral rim anteriorly,

EXPLANATION OF PLATE 70

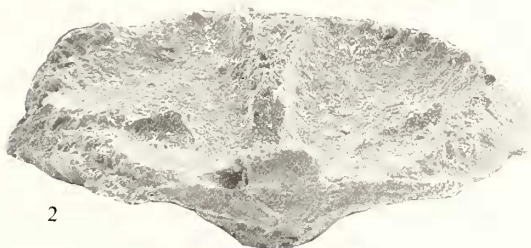
Figs. 1–9. Stereoscan photomicrographs of specimens of *Mimikonstantia sculpta*. gen. et sp. nov. All figures are of specimens coated with evaporated gold before photography. Figs. 1, 3, and 5 illuminated from lower right. 1, 2, brachial and posterior views of an early juvenile brachial valve BB 84695 showing the essentially moorellinid character of the initial median septum, $\times 60$. 3, 4, brachial and posterior views of a juvenile brachial valve BB 84696 showing the greatly thickened anterior of the median septum, $\times 40$. 5, brachial view of an adolescent brachial valve BB 84697 at the two auxiliary resorption lobe phase of development, $\times 35$. 6, posterior view of the same specimen to show the nature of the newly formed embayments, $\times 35$. 7, posterior view of the holotype showing how enlargement of the auxiliary resorption lobes results in the gradual elimination of the earlier characters. Last-formed embayments are 'stepped' relative to earlier lobes, $\times 25$. 8, angled brachial view (backward rotation 30°) of a complete shell BB 84698 from which the brachial border flange has been removed to reveal the tubercles projecting round the inner surface of the free ventral wall, $\times 25$. 9, enlargement of a pedicle valve tubercle showing the granular tubercle core (arrowed) ensheathed in secondary fibres, $\times 500$.



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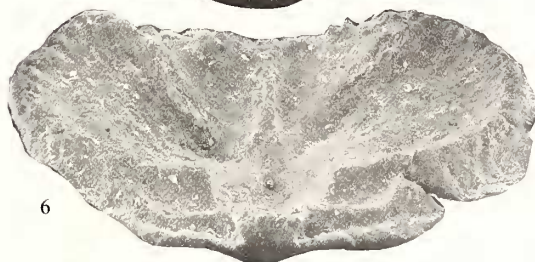
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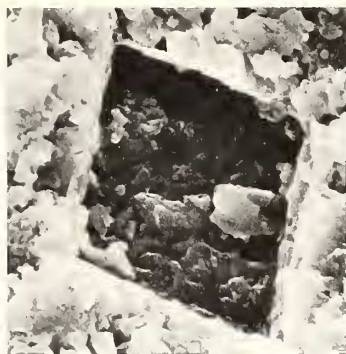
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possess on their ventral edge a posteriorly directed blade-like extension which curves backwards and downwards almost to reach the margin of the body cavity. The brachial cavities are usually smooth but in a few individuals contain a few small, low tubercles situated in a postero-lateral position (Pl. 69, fig. 1). Most adult brachial valves retain a residual boss of unresorbed shell almost in the centre of the valve floor and this sometimes retains a connection with the most centrally placed septum. Shell resorption gives the broken septa a somewhat stubby appearance (Pl. 70, fig. 5). The sub-peripheral rim is not strongly developed and in anterior and antero-lateral regions is often almost breached as a result of resorptive activity (Pl. 69, fig. 3; text-fig. 1A). The outer margin of the sub-peripheral rim is variably ornamented with tubercles, usually most strongly developed in the postero-lateral regions. A fairly wide but very thin and fragile border is present. This is invariably incomplete in separated valves and is usually damaged in complete shells also. In the latter case this results in the exposure of the characteristic marginal rim of the pedicle valve (Pl. 69, fig. 7) which greatly facilitates identification.

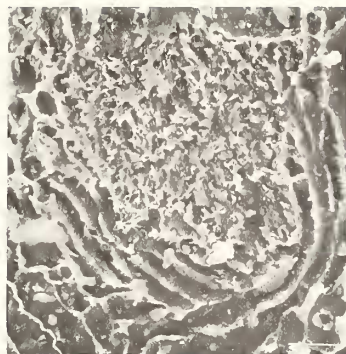
Ontogeny. Juveniles have a sub-circular outline but as a result of the characteristic growth pattern of the brachial valve (described later), the length:width ratio decreases with increasing size. However, the main feature of the ontogeny of *Minikonstantia sculpta* is the mode of development of the brachial apparatus, a feature which immediately separates the species from *Moorellina granulosa* (Moore) and *M. dundriensis* (Rollier) with which it is associated. As previously noted there are no brachial lobes in the sense that the brachial supports did not originate from the floor of the brachial cavities. The brachial supports were essentially the product of a complex shell accretion/resorption regime acting on a modified median septum. In the earliest growth stages (Pl. 70, figs. 1, 2) the median septum, although well developed, was essentially moorellinid in that it formed a blade-like partition between the left and right brachial cavities. The resorption regime of the developing cavities proceeded normally (Baker 1970) up to a brachial valve width of about 1.5 mm. At that stage the anterior portion of the median septum began to widen rapidly so that a triangular area of greatly thickened shell was produced (Pl. 70, figs. 3, 4; text-fig. 2c). Soon after its formation, this triangular area was invaded by a succession of auxiliary resorption lobes which developed sequentially from the main resorption fronts responsible for the enlargement of the brachial cavities. The first resorption front to invade the median septum extended from either the left or

EXPLANATION OF PLATE 71

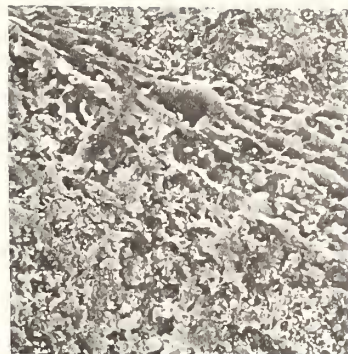
Figs. 1–8. Stereoscan photomicrographs of gold-coated cellulose acetate peels (except figs. 1 and 5) of sectioned specimens of *Mimikonstantia sculpta* gen. et sp. nov. 1, enlargement of an apparent pore on the internal surface of specimen BB 84692 enabling it to be identified as a rhomb-shaped pit. The origin of these pits remains unknown but it is assumed that they are diagenetic, probably pressure-solution, phenomena, $\times 3,500$. 2, section through the sub-peripheral rim of specimen BB 84699, showing a granular tubercle core in cross-section, deflecting secondary fibres. Section orientation: parallel with the plane of the commissure. Section location: brachial valve, anterior sector; $\times 800$. 3, section passing obliquely through the shell adjacent to the sub-peripheral rim of the same specimen, showing the relatively very thin secondary fibrous layer with granular calcite above and below it. Section orientation: as fig. 2. Section location: lateral sector; $\times 600$. 4, section passing obliquely through the sub-peripheral rim and a lateral septum of specimen BB 84698 showing the primary layer (lower), the tubercle cores associated with the secondary fibrous layer, and the inner granular calcite layer continuous with the granular calcite of the lateral septum (upper centre). Section orientation: parallel with the plane of the antero-lateral surface of the pedicle valve, intercepting the commissural plane at approximately 60° . Section location: brachial valve, right antero-lateral sector; $\times 250$. 5, floor of an auxiliary resorption lobe of the holotype showing detail of the granular calcite of which the thickened median septum is composed, $\times 3,500$. 6, section showing a granular tubercle core of pedicle valve BB 84700 in cross-section. Section orientation: horizontal, perpendicular to the shell surface. Section location: free ventral wall, anterior sector; $\times 700$. 7, section showing the granular tubercle cores and ensheathing secondary fibres in longitudinal section. Section orientation: transverse, parallel with the axis of the tubercle cores at an angle of approximately 3° from the shell surface. Section location: free ventral wall, pedicle valve, anterior sector; $\times 500$. 8, section showing the relatively thick inner granular layer, left, in the lateral sector of the pedicle valve. Section orientation: horizontal, perpendicular to the surface of the free ventral wall; $\times 500$.



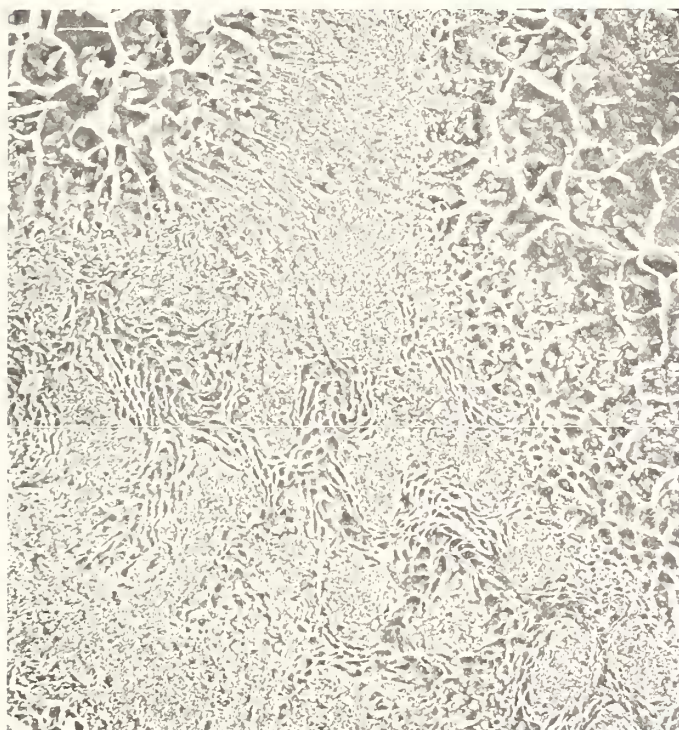
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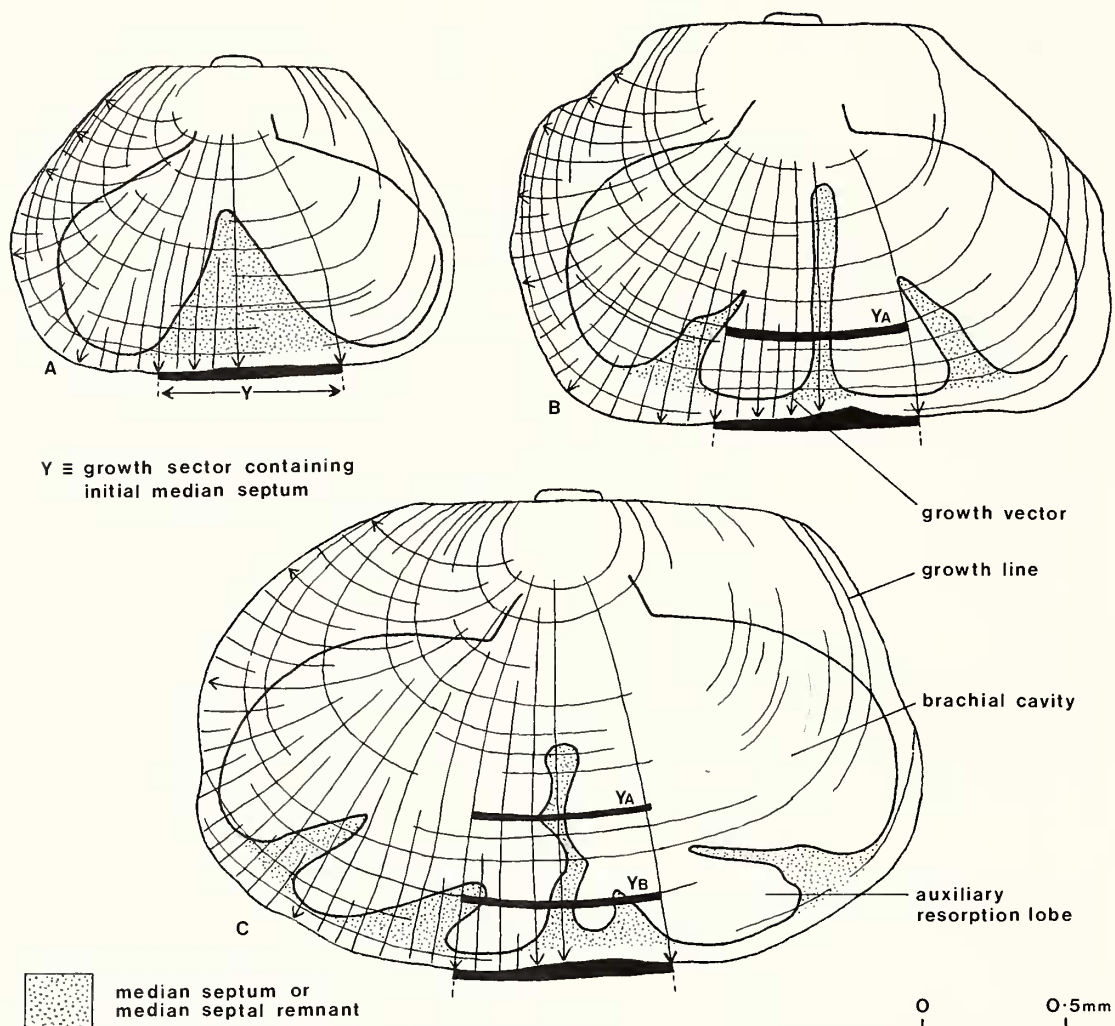


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right brachial cavity and its effect was to isolate a strip of material (median septal remnant) from the original triangle (text-fig. 2D₁, D₂). As the shell continued to increase in size the residual portion of the triangle increased in size again and was subsequently invaded by a second auxiliary resorption front (Pl. 70, figs. 5, 6). Text-fig. 2 shows that the initiation of the respective auxiliary resorption fronts followed a definite pattern which may be termed left-handed or right-handed according to which brachial cavity the first lobe was extended from. Usually the initiation of the lobes followed an alternating sequence (text-fig. 2D₁-G₁, 2D₂-G₂) but partially consecutive sequences (text-fig. 2E₁-G_{1a}, 2E₂-G_{2a}) are also encountered. The order of development can be determined



TEXT-FIG. 3. Series of diagrams in which the growth lines and primary growth vectors of the right half of a brachial valve have been superimposed on to a trace of the interior of the same valve to show that the subsequent divergence of the septal elements in *Mimikonstantia sculpta* is not a function of simple growth, which remains essentially linear in the sector containing the initial median septum. A, early juvenile prior to the development of the first auxiliary resorption lobe. B, juvenile with two auxiliary resorption lobes in which lateral remnants of the median septum are beginning to migrate away from the critical growth sector as defined by YA. C, adult valve showing the continued antero-lateral migration of the septal remnants and the initiation of new auxiliary resorption lobes anteriorly. Solid black, YA, YB, locates the earlier position of the critical growth sector on subsequent growth stages.

because initially, the floor of each new embayment was at a higher level than that of the lobe from which it developed, thus a characteristic 'step' was formed (Pl. 70, fig. 7). As enlargement of the new auxiliary resorption lobe proceeded this step was gradually eliminated by the resorption of shell material. Most median septal remnants of detached brachial valves show a fracture surface (text-fig. 2). Sectioned material shows that accretion continued on their postero-ventral surfaces so that a blade-like lamina was formed (Pl. 69, fig. 6; text-fig. 1B).

Microstructure. In the presence of a granular primary layer and a fibrous secondary layer, in which the fibres are deflected by taleola-like tubercle cores, the shell microstructure is essentially similar (Baker 1970; Williams 1973) to that of other lower and middle Jurassic species. In strong contrast, however, there is a clear indication of the suppression of the secondary fibrous layer, as it is thinly developed and underlain by a further layer of granular calcite. Also the shell of *Mimikonstantia sculpta* is impunctate. Differences in organization of the fabric of brachial and pedicle valves are sufficient to warrant description of the two valves separately.

Brachial valve

Investigation shows that the tubercles of the brachial valve have short cylindrical cores of granular calcite which are continuous with, and disposed almost perpendicular to, the primary layer (Pl. 71, fig. 2; text-fig. 4B). The association of a thin sheet of secondary fibres with these tubercle cores is a characteristic and persistent feature of the shell (Pl. 71, fig. 4). The individual secondary fibres are normally fashioned *sensu* Williams (1968) and the secondary fibrous layer is particularly well developed in the inner socket ridges. The occurrence of secondary shell is restricted in *M. sculpta* compared with other lower middle Jurassic thecideidines and, in areas of the valve away from the sub-peripheral rim and inner socket ridges, may be reduced to a sheet no more than four or five fibres thick. It is underlain by a further layer of granular calcite indistinguishable from that of the primary layer (Pl. 71, figs. 3, 4, 8). Study of the microstructure of juvenile brachial valves indicates that development of this inner granular layer is initiated at about the time that the accelerated thickening of the median septum occurs during ontogeny. It is this thick triangular-shaped area of granular calcite (Pl. 70, fig. 3) which is sculpted by the resorption lobes to leave isolated patches standing out as septal lamellae (text-fig. 2D-G). Material continues to be accreted to these lamellae so that the brachial elements are composed entirely of granular shell material (Pl. 71, figs. 4, 5). The inner granular layer is not confined to these areas, however, as horizontal sections through adult valves show that it is developed all over the floor of the brachial and body cavities, especially between the inner socket ridges. Owing to the influence of resorptive activity during growth the brachial valve remains relatively thin. The resorption regime coupled with the very thin secondary fibrous layer probably imparts an inherent weakness to the valve, as indicated by the high proportion of cracked and broken valves encountered.

Pedicle valve

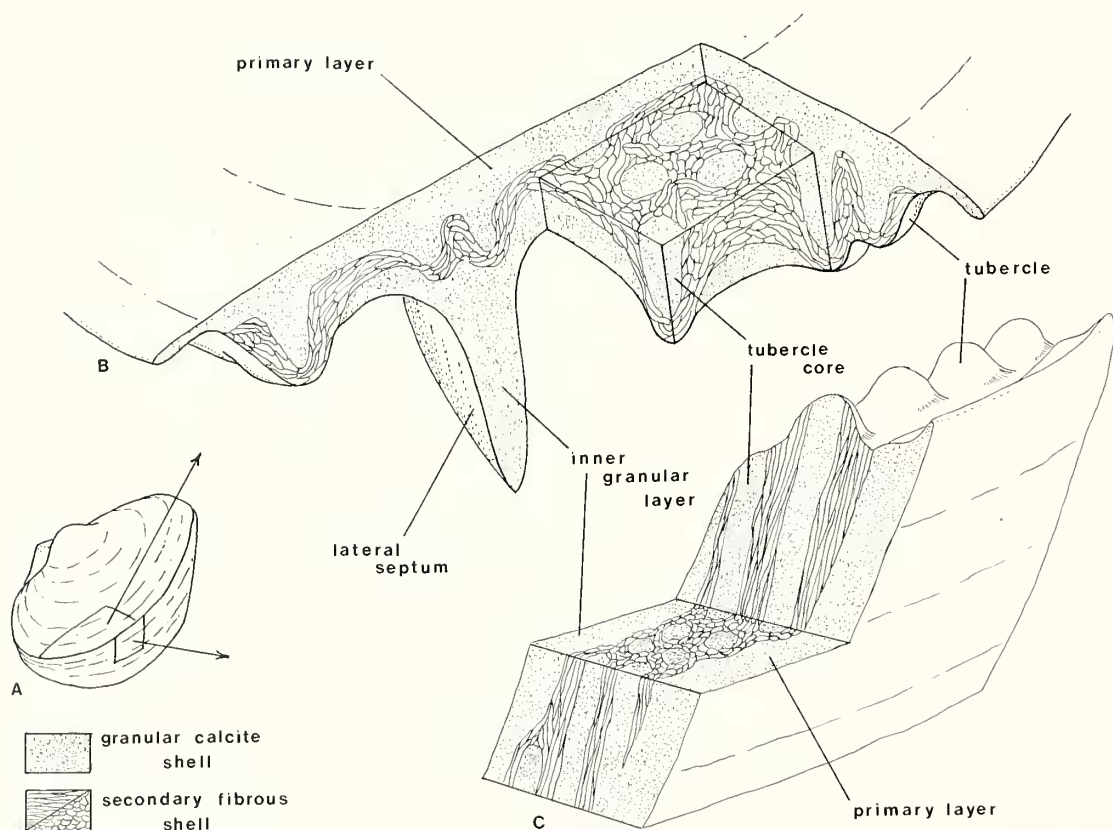
The tubercle cores of the pedicle valve are also composed of granular calcite. In contrast to those of the brachial valve, however, they form attenuated cylindrical structures (Pl. 71, figs. 6, 7; text-fig. 4C) continuous with and disposed at a low angle to (often almost parallel with) the primary layer. These granular cores, initiated in succession and ensheathed in secondary fibres, penetrate obliquely through the shell to form a row of tubercles round the inner rim of the edge of the valve (Pl. 70, figs. 8, 9). An inner granular layer is present but it does not appear to be as persistent as in the brachial valve. In anterior and antero-lateral sectors it is not sufficiently well developed to prevent the distal ends of previously formed tubercle cores from projecting through to form linear rows of ridges on the inner surface of the free ventral wall (Pl. 69, fig. 4). It is relatively much thicker in lateral sectors of the valve (Pl. 71, fig. 8) where it may attain a thickness of 65 μm .

DISCUSSION OF AFFINITY

Relationship with other genera

In general shape and characters, such as the small cardinal process and the polyseptate brachial valve, the new genus resembles an upper Jurassic form from the Volgian of the Podolian Plateau, USSR and

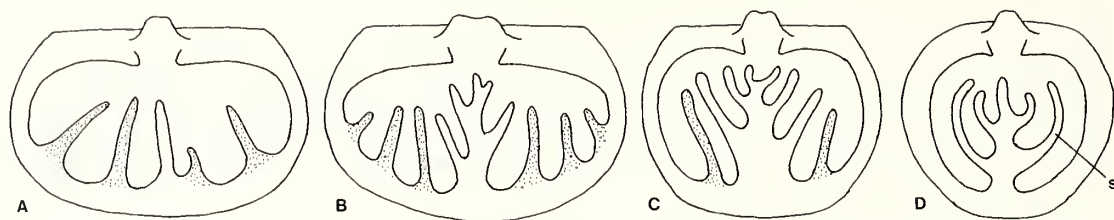
assigned to *Konstantia podolica* Pajaud 1970. Unfortunately, the validity of the original generic designation is questionable. Knowledge of the form is restricted to an account (around 1935) in an unpublished manuscript by K. Glazewski. Unhappily, the entire collection of 135 specimens referred to in the manuscript was subsequently destroyed or lost during the war. Description, text-figures, and photographs were later abstracted from the Glazewski manuscript and assigned to *Glazewskia* sp. (Glazewski and Pajaud 1964). Subsequently, Pajaud (1966) considered the species not to be a *Glazewskia* but was unable to do more than transfer it to genus X sp. A. Later, Pajaud (1970) assigned genus X to the new genus *Konstantia*, selecting *Glazewskia* sp. as the type species. At the same time he erected the species *K. podolica* (= genus X sp. A in Pajaud 1966) basing the holotype on a text-figure (graphotype) and a photograph (phototype) published in the 1964 paper. The genus and species were therefore erected on the basis of figures originating from an unpublished manuscript, a situation which led Pajaud himself to remark (1970, p. 189): 'Le binôme *Konstantia podolica* utilisé ici n'offre qu'un caractère utilitaire et ne peut être actuellement validé.' Nothing is known of the shell microstructure of *Konstantia* and the pores, presumably endopunctae, and brachial lobes identified in the Podolian specimens are not found in *Mimikonstantia*. In considering the systematic position of the new genus reference must be made to two other polyseptate genera, *Eudesella* Munier-Chalmas, 1880 and *Thecidiopsis* Munier-Chalmas, 1887.



TEXT-FIG. 4. Diagrammatic reconstruction of the shell microstructure of *Mimikonstantia sculpta*. A, locational diagram. B, block diagram showing the microstructure of the brachial valve. C, block diagram showing the microstructure of the pedicle valve.

Eudesella is first recorded from the Upper Lias, Toarcian, where it is represented by *E. mayensis* (Eudes-Deslongchamps). The species has well-developed brachial lobes and in consideration of the mode of development of the septa, Pajaud (1970, p. 184) observed that the last-formed septa were the most laterally placed, a condition which is the opposite of *Mimikonstantia*. Williams (1973) studied the shell microstructure of *E. mayensis* and concluded that the valves were lined with a continuous layer of secondary fibres. The evidence of these three characters alone is considered sufficient to separate *E. mayensis* from *M. sculpta*.

Thecidiopsis is first recorded from the Valanginian (lower Cretaceous), where it is represented by *T. cf. tetragona* Nekvasilová, 1966. The morphological resemblance between *Mimikonstantia* and *Thecidiopsis* is at first sight largely superficial because, in addition to the lateral septa, *Thecidiopsis* has a median septum divided into alternating septules. The embayments between the lateral septa are occupied by well-developed brachial lobes. Williams (1973, p. 469) studied the shell microstructure of an upper Cretaceous species *T. essenensis* (Roemer) and found the secondary fibrous layer almost completely (neotenuously) suppressed. He was only able to identify secondary fibres in the teeth and hemispondylium of the pedicle valve. A significant contribution by Smirnova (1979) provided information regarding the shell microstructure of two lower Cretaceous species, *T. tetragona* (Roemer) from the Hauterivian and *T. lata* Smirnova from the Barremian. In both species the secondary fibrous layer is almost completely suppressed in the brachial valve, being confined to the socket ridges. In the pedicle valve of *T. tetragona*, however, there is a clearly expressed secondary fibrous layer penetrated by rod-like bodies aligned almost parallel with the shell surface. In the vicinity of the muscle scars and hemispondylium the secondary layer is underlain by fine-grained acicular and granular calcite (third layer of Smirnova). In the pedicle valve of *T. lata* the secondary fibrous layer is very thin with the fine-grained inner layer better developed. The secretory regime of *Thecidiopsis* is therefore very similar to that of *Mimikonstantia* and, logically, may be regarded as further progress towards the ultimate suppression of the secondary fibrous shell layer. In addition, the polyseptate anterior of the two genera may not be as dissimilar as it appears. Study of the growth pattern of the brachial valve of *M. sculpta* (text-fig. 3) shows that as it increases in size the zones of maximum growth acceleration (Baker 1970, p. 78) associated with the initial brachial cavities (text-fig. 3A, B) become increasingly separated from the median septum. At about the four auxiliary resorption lobe phase (text-fig. 3C) the growth of the major portion of the anterior border has become essentially linear so that in order to make room for subsequent divisions, migration of the septal remnants must now be almost at right angles to the direction of growth of the shell. Thus it appears that although there seems to be no theoretical limit to the number of septal remnants which can be formed in *M. sculpta*, in practice the number is limited, through mechanical considerations, to a maximum of five. If a similar constraint operated in *Thecidiopsis*, the simplest mechanism for the formation of further septal elements would be the continuation of the resorption regime back along the sides of the median septum which would result in the development of a succession of embayments alternating on either side. As in *M. sculpta*, further accretion on the septal remnants would result in the characteristic *Thecidiopsis*-type septules (text-fig. 5B). Therefore, in terms of their mechanical requirements it is easy to reconcile the septal development pattern of *Mimikonstantia* with that of *Thecidiopsis* and also, by tachygenetic elimination of the lateral septa, with the development of the thecidiolophe of upper Cretaceous genera with sub-circular brachial valves such as *Backhausina* and *Thecidea* (text-fig. 5A-D). Thus, on the basis of morphology and ontogeny there appears to be a close relationship between *Mimikonstantia* and *Konstantia* and also, on the basis of morphology, ontogeny, and shell microstructure, between *Mimikonstantia* and *Thecidiopsis*. Pajaud (1970, p. 82, fig. 31) considered the possibility of the derivation of *Thecidiopsis* from *Konstantia*, but in the phylogeny proposed he actually derived *Thecidiopsis* from *Bosquetella*. This is thought to be an error since Pajaud states quite clearly (1970, p. 77) that *B. campichei* 'represents in no way a young stage of *T. tetragona*'. The error is all the more unfortunate since it is perpetuated in the phylogenetic chart of Williams (1973, p. 468, fig. 100). The link between *Mimikonstantia*, *Konstantia*, and *Thecidiopsis* is substantiated by the present study. Pajaud tentatively derived *Konstantia* from *Rioultina* stock, a view no longer tenable owing to the fact that *Mimikonstantia* pre-dates *Rioultina*.



TEXT-FIG. 5. Diagrams to show the possible sequence (A-D) of events in the development of a thecidolophous form from a ptycholophous ancestor through the elimination of lateral septa (stippled) and the development of septules (s) on the median septum. A, *Mimikonstantia sculpta*, Aalenian. B, *Thecidiopsis tetragona* (Roemer), Valanginian. C, *Backhausina rugosa* (d'Orbigny), Cenomanian. D, *Thecidea papillata* (Schlotheim), Maastrichtian.

In addition, there is no trace of any structure even remotely resembling the characteristic rioulitid brachial lobes in the ontogeny of either *Mimikonstantia* or *Konstantia*. The absence of brachial lobes in *Mimikonstantia* would appear to eliminate *granulosa*-type moorellinids from an ancestral role. The clear development of the polyseptate condition from an early monoseptal phase does suggest origin from monoseptal stock and descent from a Liassic ancestor of *Moorellina bouchardi*-type remains a possibility.

In view of the uncertainty surrounding the validity of *Konstantia*, the complete lack of knowledge regarding its shell microstructure, its different stratigraphic and geographic distribution and, above all, the absence of any specimens for comparative study, it is considered inappropriate to assign the new species to that genus. However, in view of the morphological similarity in their brachial valves and particularly in the similarity of the septal development pattern, it is probable that there was a genetic link between the two forms. Indeed, it is possible that the early middle Jurassic representatives are very close to the ancestral stock from which the upper Jurassic forms were derived. In recognition of this, the genus *Mimikonstantia* is proposed to include the Aalenian species.

Relationship with other species

A supposed lower Cretaceous species, *K. inexpectata* Nekvasilová, 1976, is equally problematical because the figured specimens show the development of interbrachial lobes characteristic of a *Thecidiopsis*. Admittedly in *K. inexpectata* the septal arrangement lacks the median septum with septules of species such as *T. digitata* (Sowerby) but neither is that a feature characteristic of species such as *T. bohémica* Backhaus. In his account of the ontogeny of *K. podolica*, Pajaud (1970, p. 191) suggested that the original (median) septum divided to form two junior septa ('septes-fils') one of which migrated to a lateral position, the other assuming the role of a new median septum. The process was then repeated until, in all, four septa had been formed. Study of Pajaud's text-fig. 82 shows quite clearly that this could only have been accomplished by resorption and that the mode of development of the polyseptate condition must have been very similar to the mechanism postulated for *M. sculpta*. This can not be confirmed, however, owing to the unfortunate loss of the entire collection of *Konstantia* specimens.

Walter and Almérás (1981) have described a collection of Bajocian micromorphic brachiopods from Saint-Rome-de-Cernon, France. From their morphology, it seems highly probable that specimens figured (Walter and Almérás 1981, pl. 3, figs. 11, 17-20, 22, 24, 28) as *Moorellina granulosa* (Moore) would, if investigated more closely, need to be reassigned to a species closely allied to *Mimikonstantia sculpta*.

CONCLUSIONS

In *M. sculpta* the significance of the left-handed, as opposed to the right-handed, ontogenetic development pattern remains unknown. It seems unlikely that the feature is associated with sexual dimorphism. The variation in the order of initiation of the auxiliary resorption fronts clearly indicates, however, that *M. sculpta* represents a species in which the formation of the brachial supports had not yet stabilized into a standard development pattern and, in this respect, might represent a transitional form. The similarity in morphology, septal development and, as far as is known, the shell microstructure of *Mimikonstantia*, *Konstantia*, and *Thecidiopsis* is considered to be sufficiently strong to be indicative of a genetic relationship and it is proposed that *Mimikonstantia* should be assigned to the Thecideinae, and that *Konstantia* should be reassigned to that subfamily also. The authors do not, at the present time, wish to attach any great taxonomic significance to the impunctate condition of the shell of *M. sculpta*, since the relationship between endopunctate and impunctate representatives of other taxa remains poorly understood.

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